

THE TERTIARY ECHINOIDS OF SOUTH-EASTERN AUSTRALIA  
III STIRODONTA, AULODONTA, AND CAMARODONTA (1)

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**Abstract**

The following Australian Tertiary diadematacoïd regular echinoids are described and figured: *Salenidia tertiaria* (Tate), *Murravechinus paucituberculatus* (Gregory) gen. nov., *Strongylocentrotus antiquus* sp. nov., *Strongylocentrotus* (?) sp., *Heliocidaris ludbrookae* sp. nov., *Zenocentrotus peregrinus* sp. nov. Also described and figured are fragments which indicate the occurrence of generically indeterminate representatives of the aulodont family Diadematiidae and of the camarodont family Toxopneustidae.

**Introduction**

This paper continues the description of the Tertiary echinoids of SE. Australia (Philip 1963b, 1964). Included in this part are all diadematacoïd regular echinoids excepting representatives of the camarodont family Temnopleuridae which will be dealt with in Part IV. The echinoid classification used in this series of papers has been outlined in detail elsewhere (Philip 1965). The continued assistance of the individuals mentioned in previous parts is gratefully acknowledged. A University of New England Research Grant has made continuation of the work possible.

**Systematics**

Superorder DIADEMATACEA  
Order STIRODONTA Jackson  
Suborder CALYCINA Gregory  
Family SALENIIDAE L. Agassiz  
Subfamily SALENIINAE Mortensen  
Genus *Salenidia* Pomel

*Salenidia* Pomel 1883, p. 94.

*Pleurosalenia* Pomel 1883, p. 94.

*Salenidia* Pomel, Mortensen 1935, p. 347 (cum synon.).

TYPE SPECIES: *Salenia gibba* Agassiz, the first species listed by Pomel (*loc. cit.*) and apparently designated by Lambert and Thiéry (1910, p. 212). The type species of *Pleurosalenia* Pomel is *Salenia tertiaria* Tate, by monotypy.

DIAGNOSIS: Saleniinids with simple ambulacra, each plate with a large primary tubercle.

DISTRIBUTION: Lambert and Thiéry include 8 species in this genus (recognized as a subgenus of *Salenia*), which thus ranges from the Albian of Europe to the Eocene of India and Australia. The Australian species is listed by Lambert and Thiéry as occurring in the Miocene, but it is a restricted Upper Eocene form.

REMARKS: Different interpretations have been given the genus *Pleurosalenia* Pomel. After a brief diagnosis Pomel includes within the genus '*P. tertiaria* (Tate sp.) est fossile d'Australie. *S. varispinosa* W. Tomps. (non A.Ag.) paraît être du même genre et vit dans les mers actuelles'. As *S. tertiaria* is the only species definitely included in the genus, it would seem to be the type species by monotypy. Lambert and Thiéry (1910, p. 213), however, interpret *Pleurosalenia* through *S. varispinosa* (although they designate no type species) and so regard the genus

as a synonym of *Salenocidaris* A. Agassiz. On the other hand Mortensen (*loc. cit.*) places *Pleurosalenia* in the synonymy of *Salenidia*, where it correctly belongs, for *S. tertiaria* cannot be distinguished from the type species of *Salenidia* (which genus has page priority in Pomel 1883) by more than specific differences.

### *Salenidia tertiaria* (Tate)

(Pl. 26, fig. 10-15; Fig. 2 a-b)

*Salenia tertiaria* Tate 1877, p. 256, fig. 2 a-c.

*Pleurosalenia tertiaria* (Tate), Pomel 1883, p. 94.

*Salenia tertiaria* Tate, Duncan 1887, p. 412-13.

*Salenia tertiaria* Tate 1891, p. 274 (*cum synonym.*).

*Salenia globosa* Tate 1891, p. 279.

*Salenia tertiaria* Tate, Bittner 1892, p. 334-4, Pl. 1, fig. 6-7.

*Salenia* (*Salenidia*) *tertiaria* (Tate), Lambert and Thiéry 1910, p. 212.

*Salenidia tertiaria* (Tate), H. L. Clark 1946, p. 304-5.

*Salenidia globosa* (Tate), H. L. Clark *op. cit.*, p. 305.

DIAGNOSIS: A moderately large species of *Salenidia* with an unornamented apical system, prominent primary interambulacral tubercles and wide, closely ornamented interporiferous tracts and interambulacral midzones.

TYPE SPECIMENS: Tate's original specimens were presented to the Geological Society of London and are now in the British Museum (Nat. Hist.) (BM GSL 14084). There are 5 reasonably complete specimens so labelled which may be regarded as syntypes of the species. Of these, GSL 14084a, the largest specimen which may well be the specimen figured by Tate, is selected as lectotype.

A tablet in the Tate Collection labelled '*Salenia globosa* Tate' bears the two syntypes of this nominal species. The larger, more complete of these (AUGD T275B), which agrees with the measurements originally given by Tate for the species, is here designated lectotype of *Salenia globosa* Tate.

SYNOPSIS OF MATERIAL: Some 200 specimens were examined in different collections.

DISTRIBUTION: All available specimens from SE. Australia are from the St Vincent Basin sequence, and appear to have come solely from the Tortachilla Limestone of Upper Eocene age. The species is known also from the Eucla Basin, whence it is recorded by Tate (1891) and Singleton (1941, p. 15) as occurring at Wilson's Bluff i.e. from the Wilson's Bluff Formation. Dennant and Kitson (1903) record the species from 'Ninety Mile Desert'. There are also 3 poorly preserved specimens in the National Museum Collection from the 'cliffs at Israelite Bay, southern Western Australia'.

REMARKS: This well-marked species of *Salenidia* has been described at length by Tate (1877, 1891) and Bittner (1892) so that a further detailed description is deemed unnecessary. The species is characterized particularly by the prominent interambulacral tubercles and the wide granular interporiferous tracts of the ambulacra. In these features it recalls *Salenidia blanfordi* (Duncan and Sladen 1882, p. 29-31, Pl. 6) from the Eocene of Sind, which, however, possesses a much smaller apical system in which ocular I contributes to the circle of plates around the periproct. Duncan (1887, p. 412-3) has noted that this latter feature is occasionally seen in *S. tertiaria*, but it has not been observed in any specimen available to me. Although a considerable variation obtains in the size and number of the sutural fosses of the apical system, the relative size and arrangement of the plates appears to be very constant, as, indeed, was found by Bittner.

Tate (1891) distinguished two species from Aldinga. The second, *S. globosa*, was distinguished from *S. tertiaria* by its larger size, 'its globose form, and having

seven, in place of six, primary tubercles in each row'. In fact, the lectotype of *S. tertiaria* here chosen is a large high-tested form with 7 or more interambulacral plates in each column (Fig. 1), so that *S. globosa* must be regarded as a junior synonym of *S. tertiaria*.

However, it is evident from Tate's identifications of other specimens that he intended *tertiaria* to be applied to small flattened specimens. Many authors have noted the deceptive change in shape of the corona which accompanies the growth of saleniids. For example Cooke (1959, p. 13) observes 'Young individuals commonly appear to be more depressed than mature ones . . . As the coronal plates increase in size and number, the shape of the test becomes more nearly globular'. It would seem likely, therefore, that the larger globose forms are merely growth variants of the smaller forms with low tests.

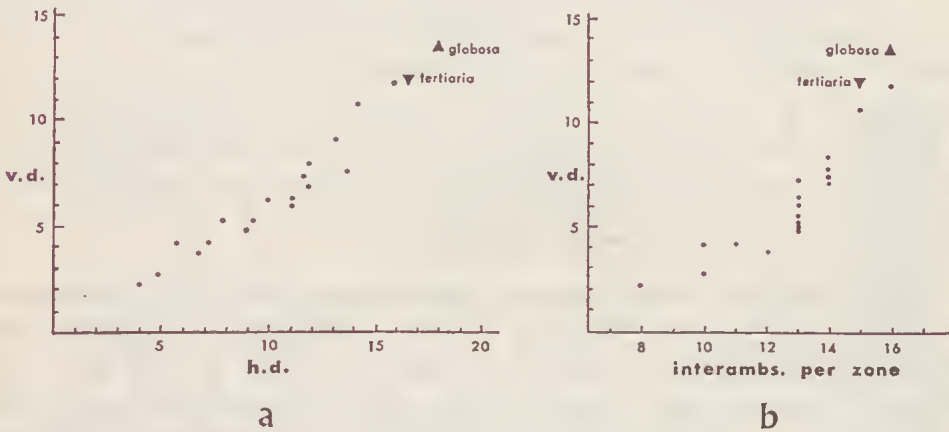


FIG. 1—Growth relationships in a collection of specimens of *Salenia tertiaria* (Tate). Superimposed are the positions of the lectotypes of *S. tertiaria* and *S. globosa* (Tate). Based on AUGD 17010 A-R.

Sufficient material is available to give a growth series for the species. Fig. 1a shows the arithmetic plot of v.d. against h.d. and Fig. 1b is the plot of v.d. against the number of interambulacral plates in each interambulacral zone. Superimposed are the positions of the lectotypes of *S. tertiaria* and *S. globosa*. It can be seen that *S. globosa* is based on a very large specimen which shows the culmination of the growth trends exhibited by the sample. Noteworthy in Fig. 1a is the change in the ratio v.d./h.d. during growth. In small specimens it is about 0.5; in large specimens it is about 0.75.

The perignathic girdle of *S. tertiaria* consists merely of small distant, styliform auricles. Its character was originally made known by Bittner (*loc. cit.*) but *S. tertiaria* is still the only species of *Salenia* in which the girdle has been described.

Suborder ARBACINA Gregory

Family ARBACIIDAE Gray

Genus *Murravechinus* (Tate MS.) gen. nov.

*Murravechinus* Tate MS. 1888, p. 251.

*Coelopleurus* L. Agassiz, Gregory 1890, p. 486.

*Murravechinus* Tate MS. 1891, p. 272, 274; 1893, p. 191.

*Coelopleurus* L. Agassiz, Lambert and Thiéry 1914, p. 264. (*partim.*)

*Coelopleurus* L. Agassiz, Mortensen 1935, p. 605 *et seq.* (*partim.*)

TYPE SPECIES: *Coelopleurus paucituberculatus* Gregory 1890, p. 486-7, Pl. 14, fig. 4-5 (= *Murravechinus spinosus* Tate MS.).

DIAGNOSIS: A *Coelopleurus*-like form in which the subambital interambulacral plates possess greatly reduced primary tubercles so that each plate is ornamented with 2 or 3 small tubercles and smaller granules. The perignathic girdle consists of slender, distant auricles.

REMARKS: Tate (1888) originally introduced the manuscript name *Murravechinus* for this handsome arbaciid, but later (1891, p. 272) wrote that this was identical with the species which had then been described by Gregory as *Coelopleurus paucituberculatus*.

Although Gregory's original description was based on a single imperfect specimen, he noted the important distinction of this form from species of *Coelopleurus*, namely the absence of primary tubercles in the interambulacra. This peculiarity did not escape Mortensen (1935, p. 608-9, p. 612) in the compilation of his encyclopaedical monograph. He noted that this Australian species thus stood well apart from the other species included in *Coelopleurus* and 'that the species might rather form the type of a separate genus' should it prove to be as described by Gregory. Mortensen even sought to examine the type specimen which had been lodged by Gregory in the Ipswich Museum, but found that it had been lost. Topotype material now establishes that Gregory's description was accurate in all detail. Consequently Tate's MS. name *Murravechinus* is here validated as a generic category to contain this single species.

Mention should be made of the genus *Sykesia* Pomel (1883, p. 88) diagnosed as possessing 6 series of interambulacral tubercles, which would suggest close comparison with *Murravechinus*. However, *Sykesia* was based on the figures of *Coelopleurus pratti* d'Archiac (d'Archiac and Haime 1853, Pl. 13, fig. 5-6). The subsequent description and illustration of the species (Duncan and Sladen 1885, p. 254-257, Pl. 39, fig. 9-12) shows the interambulacra to possess two series of large primary tubercles as in typical species of *Coelopleurus*. Lambert and Thiéry (1914, p. 264) note 'Les tubercules secondaires du *C. Pratti* résultent seulement de la restauration d'un individu très défectueux en sorte que le genre *Sykesia* n'a aucune valeur réelle'.

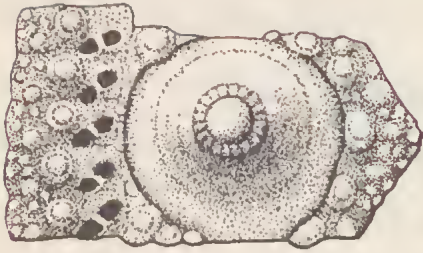
The excessive enlargement of the ambulacral tubercles relative to those of the interambulacra in *Murravechinus* leads to the ambulacra being slightly wider than the interambulacra at the ambitus, unlike fossil species of *Coelopleurus*. A further outcome of this peculiarity is the fact that there are considerably more interambulacral plates than ambulacral plates in adjacent columns.

Attention may also be directed to the extremely delicate auricles of *Murravechinus* (Fig. 2d). In *Coelopleurus* the girdle, although variable, in general consists of auricles united above the ambulacra. In *Murravechinus* these are very thin processes, widely separated at their extremities. They are so delicate that they were found almost impossible to free from the soft matrix without damage.

Undoubtedly *Murravechinus* represents a specialized offshoot from *Coelopleurus*

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FIG. 2—*a-b Salenidia tertiaria* (Tate). *a*, Ambital interambulacral plate and adjacent ambulacra column (AUGD 17012); *b*, Apical system (AUGD 17011),  $\times 6$ . *c-d, f-g, Murravechinus paucituberculatus* (Gregory). *c*, Arbacioid compounding of ambital ambulacral plates. Note irregularity in position of pore-pairs in components (P 17958),  $\times 6$ ; *d*, Slightly damaged auricles (P 18321),  $\times 10$ ; *f*, Apical system (P 17955),  $\times 6$ ; *g*, Adoral terminations of an ambulacral and interambulacral zone. Note prominent 'tags' of the gill slits (P 17957),  $\times 6$ . *e*, Diadematid gen. et sp. indet. Proximal portion of radiole (P 22308),  $\times 6$ .



a



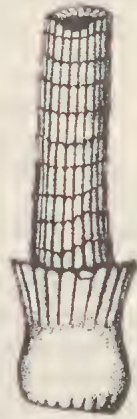
b



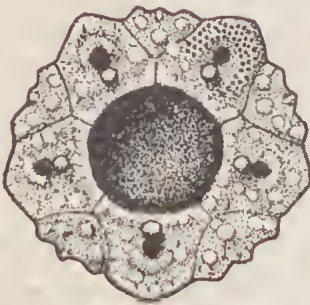
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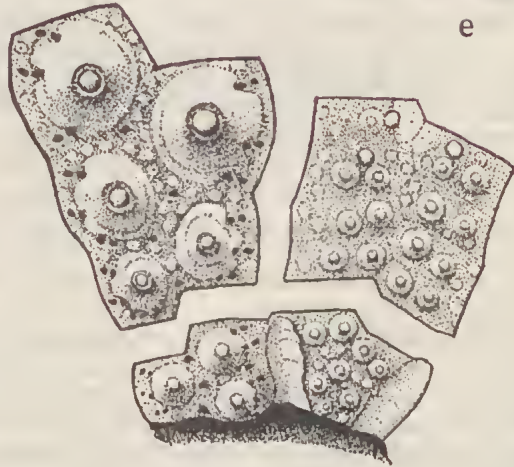
d



e



f



g

which, in middle Tertiary times, was present in India. *Coelopleurus* itself is represented in the living Australasian fauna by *C. australis* H. L. Clark, known only from Bass Strait. This is a typical species of *Coelopleurus*, very closely related to the South African *C. interruptus* Döderlein.

### **Murravechinus paucituberculatus** (Gregory)

(Pl. 26, fig. 1-9; Fig. 2 c-d, f-g)

*Coelopleurus paucituberculatus* Gregory 1890, p. 486-7, Pl. 14, fig. 4-5.

*Coelopleurus paucituberculatus* Gregory, Tate 1891, p. 274.

*Murravechinus spinosus* Tate MS., *loc. cit.*

*Coelopleurus paucituberculatus* Gregory, Mortensen 1935, p. 608-9, p. 612; H. L. Clark 1946, p. 306.

DIAGNOSIS: As for genus.

TYPE SPECIMEN: The only described specimen to date is the holotype figured by Gregory (*loc. cit.*) from the 'banks of the Murray River at Morgan' i.e. the Morgan Limestone. Gregory states that this specimen is lodged in the Ipswich Museum. Mortensen (*loc. cit.*) instituted a search for it, but records the specimen to be lost. Mr H. E. P. Spencer, the present curator of the Ipswich Museum, at my request kindly undertook a further search for the holotype, but this was unsuccessful.

Nine topotype specimens (P 17955-63) are in the collection.

DESCRIPTION: The test is low and depressed and somewhat pentagonal in outline, with the naked area of the interambulaera extending to the ambitus. The gill-slits are very shallow, but prominent 'tags' are present extending from the margin of the peristome to opposite the base of the third ambulaeral plate from the peristome (Fig. 2g).

The apical system (Fig. 2f) is comparatively small and regularly dicyclie, with the madreporite not enlarged. The genital pores are large, and a prominent granule is mounted between these and the periproct; a similar, although smaller granule is present toward the centre of each of the oculars, which appear to possess double perforations as in *Coelopleurus*. The apical system is closely yet obscurely ornamented by small, low granules as shown in Fig. 2f.

The ambulaera are relatively broad, with the primary tubercles gradually increasing in size to the ambitus. Both the ambulacral mid-zone and the adradial zone are narrow, and each bears small, low, secondary tubercles. The pores are mounted close to the adradial suture and are uniserial, although they tend to be somewhat arcuate on the larger plates. The components of the ambulacral triads are typically abraeoid in arrangement (Fig. 2c). The smooth imperforate ambulaeral tubercles are large and high at the ambitus, with the well-defined margins of the areoles notched by the pore-pairs, the inner of which may even lie within the boss. Up to 7 sphaeridial pits (from which the spaciaria have been lost in all specimens) are present in each ambulaeral mid-zone, arranged in series originating at the margins of the peristome.

The interambulacral plates are low, and below the ambitus each zone is ornamented with 4-6 irregular series of small tubercles, the inner of which is usually the largest and so probably represents the primary tubercle. Toward the adradial suture the tubercles are smaller and low tubercles are present covering the plates. The bare median zones of the interambulacra are slightly sunken and bordered by well-defined granules which form regular vertical series which may extend on to the oculars. On each plate a small tubercle is mounted beside the granule, on the adradial side of which are smaller tubercles.

## SYNOPSIS OF MATERIAL:

From the Murray River Cliffs:

'Lower beds, Morgan', Morgan Limestone, P 17955-63, Batesfordian and Baleombian.

'Lower beds, between Wongulla and Mannum', Mannum Formation, P 18321-2, Longfordian.

## MEASUREMENTS:

No.	h.d.	v.d.	Diam. apical system	Diam. peri- stome	No. ambis	No. interambis
P 19756	10.0 mm	5.0 mm	3.0 mm	4.2 mm	7	11
P 19757	15.5	9.0	5.0	6.5	9	13(14)
P 19755	17.5	9.2	6.0	7.5	10	14
P 19758	19.5	9.5	6.5	—	10(11)	14

Order AULODONTA Jackson

Suborder DIADEMINA Dunean

Family DIADEMATIDAE Gray

Gen. et sp. indet.

(Fig. 2 e)

MATERIAL AND HORIZON: Radiole P 22308, 'Curlewis, Viet.', horizon and age not assignable, almost certainly Miocene.

DESCRIPTION AND REMARKS: The specimen is the proximal portion of a radiole 7.5 mm long. The base is expanded, with an oblique, distinctly erenulate acetabulum and a flaring milled ring. The shaft is hollow and is marked by longitudinal grooves and distinct verticellation in which the segments tend to be horizontally aligned.

The diadematid affinities of this radiole are indicated by the hollow shaft, its verticellation and erenulate acetabulum. As diadematids constitute a significant element of present-day subtropical Australian faunas, it is surprising that this fragment is the only known indication of the occurrence of the family in the Tertiary of SE. Australia. Diadematids, however, are seldom found fossilized presumably because their imbrication leads to rapid post-mortem disintegration of the test.

Order CAMARODONTA Jackson

Suborder TEMNOPLEURINA Mortensen

Family TOXOPNEUSTIDAE Troeschel

Gen. et sp. indet.

(Pl. 29, fig. 4-5)

MATERIAL AND HORIZON: Two test fragments, P 18865, 18868, 'Airey's Inlet', i.e. Point Addis Limestone of Janjukian age.

DESCRIPTION AND REMARKS: The larger of the two fragments (Pl. 29, fig. 5) suggests that the test of this form was low and grew to a h.d. of about 50 mm. The ambulaera are of echinoid triads in which the pore-pairs are distinctly arcuate above the ambitus. Adorally the arcs become progressively lower, the poriferous traets are correspondingly widened and the pore-pairs triserial. The smooth imperforate primary tubercles of the ambulaera form regular vertical series, and irregularly

placed secondary tubercles surround the areoles of the primary tubercles. The interambulacra also possess regular vertical series of primary tubercles with an enlarged secondary tubercle each side of the primary tubercle on each plate.

Although the absence of the peristome prevents positive identification of these fragments as belonging to a toxopneustid, there can be little doubt that this is their position. The comparatively large size of the test, together with the adoral widening of the poriferous tracts of the ambulacra, prevents comparison with Australasian Echinidae, with which otherwise the fragments could be compared. From present knowledge some general relationships with such toxopneustid genera as *Cyrtechinus*, *Nudechinus*, *Gymnechinus*, and *Lytechinus* may be suggested.

On a slightly more complete fragment than either of the present specimens Duncan and Sladen (1885, p. 315, Pl. 49, fig. 5-6) based the species *Echinus subcrenatus*. This form, from the Gáj Series of Sind, was made the type species of *Gajechinus* Lambert and Thiéry (1910, p. 242) which genus was to be distinguished by the ambulacra. In the triads of these 'la plaque mediane est reduite a l'etat de demi-plaque . . .' i.e. the form possessed echinoid triads. Mortensen (1943a, p. 292) justly complains that *Gajechinus* is the 'most ill-considered' of all Lambert and Thiéry's genera.

The present fragments, although of a larger form, appear to resemble closely '*Gajechinus*' *subcrenatus*.

Suborder ECHININA Mortensen  
Family STRONGYLOCENTROTIDAE Gregory  
Genus **Strongylocentrotus** Brandt

*Strongylocentrotus* Brandt 1835, p. 63.

*Strongylocentrotus* Brandt, Mortensen 1943b, p. 103 *et seq.* (cum synonym.)

TYPE SPECIES: *Echinus (Strongylocentrotus) chlorocentrus* Brandt (= *Echinus droebachiensis* Müller), validated by Opinion 208 of The International Commission of Zoological Nomenclature.

DIAGNOSIS: Moderately large, usually thick tested, somewhat flattened echininids with polyporous ambulacra with 5 or more pore-pairs in each arc. On the adoral surface the ambulacra are of constant width and, at the margin of the peristome, are wider than the interambulacra. The apical system has oculars I and V broadly insert and a slightly enlarged madreporite. The gill slits are shallow and the perignathic girdle is of high auricles united above the ambulacra with a large foramen.

DISTRIBUTION: Mortensen (1943b) recognized 7 living species of this genus, 6 confined to the N. Pacific, and the seventh, *C. droebachiensis*, widely distributed through the Arctic Seas and southward into the N. Atlantic. In view of the remarkable variation which has been described in *S. droebachiensis*, and also in the other forms, the discrimination of the species is very difficult, and their validity highly questionable (as Mortensen admits). From the existing information no revision of these forms can be suggested, but it seems likely that only two species groups are represented in the present named forms.

Mortensen (1942, 1943b) also separated the well-marked species *S. pulcherrimus* (A. Agassiz) and *S. fragilis* Jackson respectively as the genera *Hennicentrotus* and *Allocentrotus*. It seems that these, at most, should be considered as subgenera of *Strongylocentrotus*.

As fossil, the genus has been recorded from the Miocene and Pliocene of N. America (Grant and Hertlein 1938), the Miocene of France, and Pliocene of Britain. Mortensen (1943b, p. 197) maintained that, from the published informa-



tion it cannot be decided whether or not the European forms rather belong to *Heterocentrotus*. However, examination of some British material does suggest that it is correctly located in *Strongylocentrotus*, although confusion exists as to the specific identification of the British Pliocene form.

Gregory (1891) diagnosed the species *S. scaber*, based on a test fragment from the Coralline Crag of Aldborough. Subsequently (1892b) he identified a test from the same locality as *S. droebachiensis* (Müller). This specimen (SM c31548) later became the type specimen of the species *S. cotteui* Bell (1897, p. 9). This cannot be distinguished from *S. scaber*. The fact that there are 6 pore-pairs consistently developed in the arcs of the ambulacra seems to justify the separation of this form from *S. droebachiensis* and *Heterocentrotus lividus*. The apical system is unknown, but the girdle is composed of high auricles meeting above the ambulacra with a high foramen, so that the species is best considered as belonging to *Strongylocentrotus*.

Because of the distribution of the genus, Mortensen considered it to have originated in the N. Pacific and to have migrated to the N. Atlantic in relatively recent times. The form described below, fully typical of the genus, indicates that it was established in the Australasian province in Oligocene times.

***Strongylocentrotus antiquus* sp. nov.**

(Pl. 29, fig. 1-3; Fig. 3, 4 a, d)

*Toxopneustes* sp. Tate MS. (Museum label).

DIAGNOSIS: A moderate sized, low tested species of *Strongylocentrotus* with high coronal plates and 5 (rarely 6) pore-pairs in very erect arcs. The secondary ambulacral tubercles are small.

TYPE SPECIMEN: Holotype AUGD 17014, a test from the Tate Collection labelled '*Toxopneustes*, Glenforslan', i.e. from the Mannum Formation of Longfordian age.

DESCRIPTION: The test is rather small and flattened, rounded in outline, and with a small apical system and a weakly notched, slightly sunken peristome. The perignathic girdle (Fig. 4a) is typical of the genus.

The apical system (Fig. 3a) has oculars I and V broadly insert. The madreporite is enlarged, with the porous area covering most of genital 2. The genital pores are large, and the plates are obscurely ornamented by granules.

The ambulacra are about half of the width of the interambulacra, and, because the arcs are very erect, the poriferous tracts are narrow above the ambitus. There are 5 (rarely 6) pore-pairs in each arc. The primary ambulacral tubercles are relatively large, and are surrounded by a small secondary tubercles and granules. On each ambital plate the upper inner and the lower outer secondary tubercles are slightly enlarged.

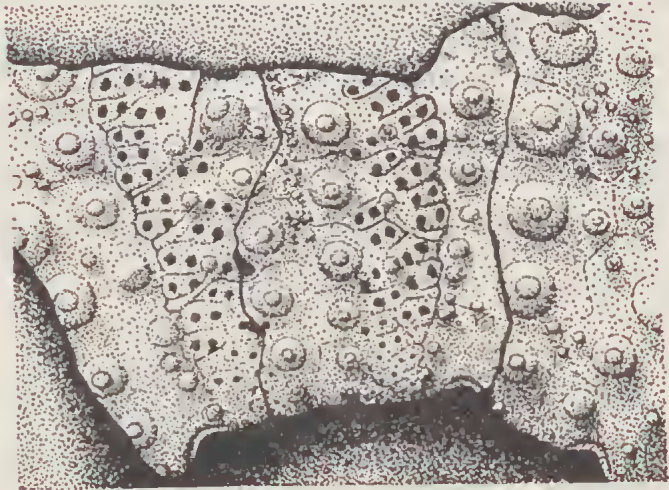
The high interambulacral plates possess slightly larger, smooth, imperforate primary tubercles which form regular vertical series. Their areoles are surrounded by closely spaced secondary tubercles and granules.

MEASUREMENTS:

No.	h.d.	v.d.	Diam. apical system	Diam. peri- stome	No. amb	No. interamb
AUGD 17014	37.0 mm	18.5 mm	7.0 mm	13.5 mm	20(21)	14(15)
P 18866	33.0	16.5	6.5	10.5	21(22)	16(17)



a



b

FIG. 3.—*Strongylocentrotus antiquus* sp. nov. a, Apical system and adapical plates of holotype; b, Adoral termination of an ambulacral column of holotype,  $\times 6$ .

## SYNOPSIS OF MATERIAL:

Mannum Formation, Longfordian: Holotype and 1 test *ex* R. J. Foster Coll., 'Right bank of Murray River, 3 m. N. of Mannum'.  
'Airey's Inlet', P 18866, Point Addis Limestone, Janjukian.

REMARKS: *S. antiquus* resembles the variable living species *S. droebachiensis* (Müller), but differs in the very erect arcs of the ambulacra. Thus on an ambital ambulacral plate only a single secondary tubercle occurs within the poriferous traet. This feature the species shares with *S. franciscanus* (A. Agassiz) (Mortensen 1943b, p. 244, fig. 106), but that form has considerably more pore-pairs in each arc. The character of the ambulacral ornament also seems to distinguish *S. antiquus* but this is described as being highly variable in *S. droebachiensis*.

Tate's museum label of the type specimen invites comparison of the species with toxopneustids. Although *S. antiquus* has little in common with *Toxopneustes* itself, it may be compared with species of the polyporous genus *Pseudoboletia*, particularly the living *P. atlantica* H. L. Clark. However, the echininid affinities of the species are indicated by the shallow gill slits. *S. antiquus* also resembles the polyporous echinid *Heterocentrotus*, particularly *H. lividus*, but, because of the character of the girdle and of the apical system the species must be placed in *Strongylocentrotus*.

**Strongylocentrotus (?) sp.**

(Pl. 29, fig. 8)

MATERIAL AND HORIZON: Test fragments from the Batesford Limestone, Longfordian or Batesfordian:

'Filter Quarry', P 18451-2; 59; 60-1; 68.

'Batesford', 3 fragments *ex* Singleton Collection.

'Ironstones above Older Basalt, just downstream from Hilbert's Pitt', P 20494 (mould of test fragment), Green Gully, Keilor, i.e. Batesfordian or Balcombian.

DESCRIPTION AND REMARKS: These fragments are all of a large, comparatively thin-tsted, polyporous echininid, with 6 pore-pairs to each arc. The h.d. probably exceeded 100 mm.

The fragments thus suggest a form different from *S. antiquus*, but there is a general similarity in ornament, which suggests some relationship with this species.

It should be pointed out that generic characters of this form are not preserved; for the present, however, it may be included in *Strongylocentrotus*.

## Family ECHINOMETRIDAE Gray

Genus **Heliocidaris** Agassiz and Desor

*Heliocidaris* L. Agassiz and Desor 1846, p. 371.

*Heliocidaris* L. Agassiz and Desor, Mortensen 1943b, p. 335 *et seq.* (*cum synonym.*).

TYPE SPECIES: *Echinus omalostroma* Valenciennes (= *Echinus tuberculatus* Lamarck), by elimination.

DIAGNOSIS: Large, hemispherical, robust echininids which have a rounded outline, and polyporous ambulacra with 7 or more pore-pairs to each plate. The arcs may be irregularly double, and the expanded poriferous traets of the flattened adoral surface are petalloid. The gill slits are shallow.

DISTRIBUTION: Mortensen (1943b) includes in the genus the two well-marked Australian species *H. tuberculata* (Lamarck) and *H. erythrogramma* (Valenciennes). Both these are widely distributed around the Australian coast.

Fossil representatives of the genus have not been described previously, although Fell (1953, p. 246) records 'some Echinometrid, possibly *Heliocidaris*' from the Eocene of New Zealand.

***Heliocidaris ludbrookae* sp. nov.**

(Pl. 27, fig. 1-4, Pl. 28, fig. 1-2; Fig. 4 c)

**DIAGNOSIS:** A large species of *Heliocidaris* which possesses up to 12 pore-pairs, arranged in 2 irregular arcs, in each compound ambulacral plate.

**TYPE SPECIMEN:** Holotype AUGD 17015 (*ex* MDSA F46/55), 'Sec. 519 Hd. Finnis, Lower member, Mannum Formation', i.e. Longfordian.

**DESCRIPTION:** The large test is thick, rounded in outline, and very flattened on the adoral surface.

On the adapical surface the irregular arcs of the pore-pairs are comparatively erect, with up to 8 pore-pairs in an outer arc and 3 to 5 in a very irregular inner arc. Toward the ambitus there are usually 10 to 12 pore-pairs to each plate. On the adoral surface the arcs become very low and the poriferous tracts are widened and petalloid, attaining almost thrice the width of the interporiferous tracts. The primary ambulacral tubercles are moderately large, their areoles surrounded by closely spaced secondary tubercles and granules. Toward the ambitus an enlarged secondary tubercle occurs at the inner angle of each plate, and another is usually present within the poriferous tract between the inner and outer arcs. Below the ambitus the primary tubercles decrease markedly in size.

The interambulacra possess regular vertical series of moderately large, smooth primary tubercles, which are joined by very irregular inner and outer series of enlarged secondary tubercles towards the ambitus. On the adoral surface the tubercles are greatly reduced in size, but the primary tubercles continue as a regular series to the peristome. The outer series of enlarged primary tubercles may be traced to the peristome, but the inner two series tend to merge and be lost half way to the peristome.

**MEASUREMENTS OF HOLOTYPE:**

h.d.	v.d.	Diam. apical system	Diam. peristome	No. amb.	No. interamb.
101 mm	45 mm	19.5 mm	26 mm	20(21)	26(28)

**SYNOPSIS OF MATERIAL:** Beside the holotype, the species is represented by the following test fragments from the Batesford Limestone:

'Filter Quarry, Batesford', P 18448; 50; 53-4; 56; 62; 64-5; 67; 71-2; 75; 77-8.

'Upper Quarry', P 19784-5.

'Batesford', 6 test fragments *ex* Singleton Collection.

**REMARKS:** Also present from the Batesford Limestone are a number of diadematacid radioles which in all probability belong to this species. They are up to 30 mm long with tapering cylindrical shafts and prominent bases with expanded and oblique milled rings. The group of radioles is P 19637-51, from the Middle Quarry at Batesford. Four of these radioles are illustrated in Pl. 27, fig. 5.

The large size of this form, coupled with the irregular doubling of the arcs of the ambulacra, serve to distinguish it from the living species of the genus. Doubling of the ambulacral arcs is only very incipiently developed in the living species, and is known principally in the genus *Heterocentrotus*.

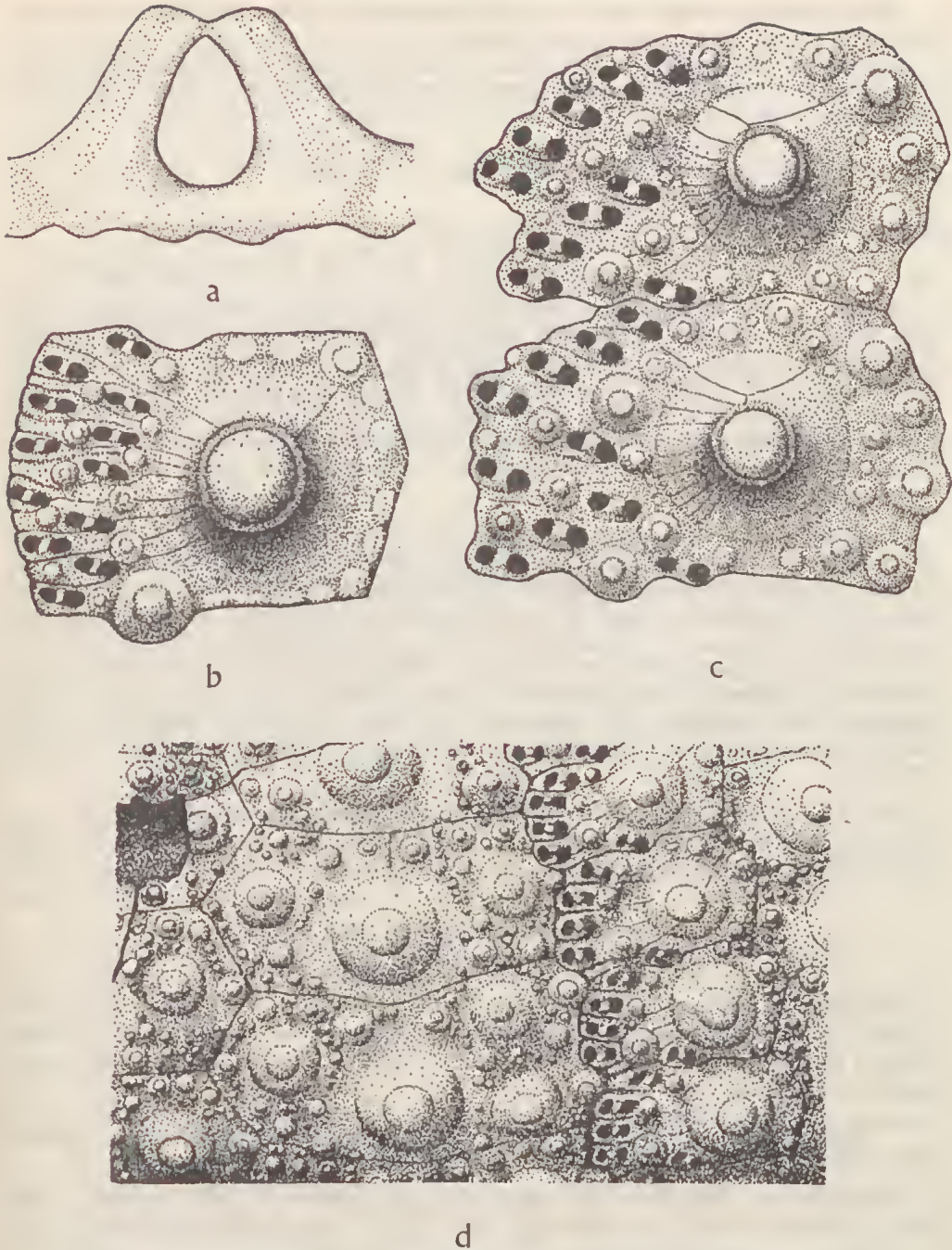


FIG. 4—*a, d*, *Strongylocentrotus antiquus* sp. nov. *a*, Auricles of holotype,  $\times 10$ ; *d*, Ambital plates of holotype,  $\times 6$ . *b*, *Zenocentrotus peregrinus*, sp. nov. Ambulacral plate (P 18480),  $\times 6$ . *c*, *Heliocidaris ludbrookiae* sp. nov. Ambital ambulacral plates of holotype (AUGD 17015),  $\times 6$ .

The species is named after Dr N. H. Ludbrook, who very kindly passed on the handsome type specimen for description.

Portion of the lantern is preserved in the hard limestone matrix within the peristome of the holotype, but it proved impossible to excavate without danger of damage to the test.

#### Genus *Zenocentrotus* A. H. Clark

*Zenocentrotus* A. H. Clark 1931, p. 5.

*Zenocentrotus* A. H. Clark, Mortensen 1943b, p. 400.

TYPE SPECIES: *Zenocentrotus kellersi* A. H. Clark, by original designation.

DIAGNOSIS: Moderately large echininids which possess a flattened adoral surface, and an ovate test outline. On the adoral surface the poriferous tracts are widened and petalloid, but above the ambitus the poriferous tracts are narrow and the pore-pairs are arranged in usually distinct double arcs with up to 12 pore-pairs to each compound ambulacral plate. The ambulacra possess only a series of prominent primary tubercles, whereas the interambulacra have enlarged secondary tubercles developed adradially to the primary tubercles. The primary radioles are comparatively stout.

REMARKS: The occurrence of this genus in the Australian Palaeogene is of considerable interest inasmuch as the geological history of the specialized polyporous echinids is greatly extended. Indeed, it is surprising to discover this genus and *Heliocidaris* ranging so far back in time. Together with *Strongylocentrotus antiquus*, and *Echinometra thomsoni* Haime (d'Archiac and Haime 1853, p. 207, Pl. 13, fig. 13 a-b) from probably Eocene rocks in India, they represent the oldest known undoubted members of the Suborder Echinina. Because of their very specialized characters (the doubling of the pore-pair arcs and the petalloid ambulacra of the adoral surface) it seems that even a more ancient origin of the group may be postulated.

DISTRIBUTION: Mortensen (1943b) recognized the two reasonably circumscribed species described by A. H. Clark (1931) from Tonga and Samoa. No fossil occurrences of the genus have been reported previously.

#### *Zenocentrotus peregrinus* sp. nov.

(Pl. 28, fig. 3-6, Pl. 29, fig. 6, 9; Fig. 4b)

DIAGNOSIS: A large species of *Zenocentrotus* which has up to 12 pore-pairs arranged in double arcs in each compound ambulacral plate. The vertical series of enlarged secondary tubercles are horizontally alternate, so that the interambulacral plates are geniculate.

TYPE SPECIMEN: The holotype is P 18867, the largest available test fragment, from 'Airey's Inlet', i.e. Point Addis Limestone of Janjukian age.

DESCRIPTION: The test was apparently large (some of the fragments from Batesford suggest a h.d. of 100 mm), and thick. The gill slits are shallow and rounded.

Above the ambitus the ambulacral plates (Fig. 4b) are high, each with a large, high, smooth primary tubercle which fills the interporiferous tract in each column. The pore-pairs are arranged in 2 erect arcs, so that the poriferous tract is only

about half the width of the interporiferous tract. Secondary tubercles (sometimes very slightly enlarged at the corners of the plates) and granules occur irregularly through the poriferous tract, and form a circlet around the areoles of the primary tubercles. On the adoral surface the arcs become very low, and the poriferous tracts are widened and petalloid, half way to the peristome reaching almost 5 times the width of the interporiferous tract. The primary ambulacral tubercles decrease markedly in size below the ambitus, but continue to the margin of the peristome as a regular series.

The interambulacra possess closely spaced tubercles of size similar to the corresponding ambulacral primary tubercles. These are arranged usually in 3 alternately placed vertical series in each column. Because of this alternation, they appear to be arrayed in diagonal rather than horizontal and vertical series. The horizontal sutures also run between the tubercles, so the plates are distinctly geniculate. The tubercles of the innermost series are the largest and represent the primary tubercles, for, on the adoral surface where the tubercles are greatly reduced in size, it is this series which can be traced to the borders of the peristome.

**SYNOPSIS OF MATERIAL:** Beside the holotype, the species is represented by the following test fragments from the Batesford Limestone:

'Filter Quarry', P 18449; 55; 57; 63; 66; 73; 76; 79; 80.

'Upper Quarry', P 19786.

'Batesford', 4 test fragments *ex* Singleton Collection.

**REMARKS:** A number of rather massive, fragmentary diadematacid radioles is present in the collection from Batesford (Pl. 29, fig. 7). These correspond well with the size of the large tubercles of this species, and in all probability belong to it. The largest is 40 mm long, but probably they were considerably longer than this. The shafts are cylindrical or flattened and are marked by closely spaced longitudinal grooves. Toward its proximal end the shaft expands slightly to a rounded milled-ring. The base is very short, and is rapidly constricted to a small acetabulum. When worn, the distal portion of the radiole is reduced to a rounded knob.

As a confident assessment of specific differences in the available test fragments is impossible, for the present the smaller, probably less highly ornamented form from Airey's Inlet must be placed with the fragments from the younger horizons at Batesford. However, as the species is at present known and defined, its generic relationships are reasonably clear.

The ambulacra, in the large primary tubercles and the consistent regular doubling of the arcs, are similar to those seen in living species of the genera *Heterocentrotus*, *Cobolocentrotus*, and *Zenocentrotus*. However, in *Heterocentrotus* the interambulacra also possess a vertical series of large primary tubercles in each column, and the huge massive radioles are fully characteristic of the genus. Furthermore, in those species of *Cobolocentrotus* which have this type of ambulacra (subgenus *Podophora*) the interambulacra are much more complexly ornamented by enlarged secondary tubercles, among which the primary tubercles may not be distinguished. The genus also is particularly characterized by the peculiar scale-like radioles.

Thus the species can be placed in *Zenocentrotus* with some degree of assurance, particularly in view of the character of the radioles from Batesford, which, although not fully typical of those of living species of *Zenocentrotus* in their rounded milled rings, are unlike those of either *Heterocentrotus* or *Cobolocentrotus*.

From living species of *Zenocentrotus*, *Z. peregrinus* is distinguished by the geniculate interambulacral plates, and the greater number of pore-pairs in the more erect, double arcs of the adapical ambulacra.

## References

(Additional to those listed in previous parts)

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## Explanation of Plates

Figures  $\times$  1 unless otherwise stated.

## PLATE 26

- Fig. 1-9—*Murraveclinus paucituberculatus* (Gregory). (1) Adapical, (2) Lateral, (3) Adoral views of P 17955; (4) Adapical, (5) Lateral, (6) Adoral views of a small specimen P 17956; (7) Adapical view of P 17955,  $\times$  2; (8) Superambital, (9) Subambital view of P 17955,  $\times$  5. Specimens from 'Morgan', Batesfordian or Balcombian.
- Fig. 10-15—*Salenia tertiaria* (Tate). (10) Lateral view of lectotype BM GSL 14084a (British Museum photograph); (11) Adapical, (12) Lateral, (13) Adoral views of lectotype of *Salenia globosa* Tate AUGD T 275B; (14) Apical system of AUGD T 1727A, showing pierced madreporite,  $\times$  5; (15) Ambital view of AUGD 17013,  $\times$  5. Specimens from the Upper Eocene Tortachilla Limestone.

## PLATE 27

- Fig. 1-4—*Heliocidaris ludbrookae* sp. nov. (1) Adapical, (2) Lateral views of Holotype AUGD 17015, 'Mannum', Longfordian; (3) Test fragments P 18472, P 18469; (4) Test fragments P 18450, P 18462, 'Batesford', Longfordian or Batesfordian.
- Fig. 5—*Heliocidaris ludbrookae* sp. nov. (?) Radioles P 19637-40, 'Middle Quarry, Batesford', Longfordian or Batesfordian.

## PLATE 28

- Fig. 1-2—*Heliocidaris ludbrookae* sp. nov. (1) Adoral, (2) Superambital view of holotype AUGD 17015,  $\times$  2.
- Fig. 3-6—*Zenocentrotus peregrinus* sp. nov. (3) Ambulacral plates P 19786, 'Upper Quarry, Batesford', Longfordian or Batesfordian,  $\times$  2; (4) Ambulacral plates P 18480, 'Filter Quarry, Batesford', Longfordian or Batesfordian,  $\times$  2; (5) Adoral, (6) Lateral views of holotype P 18867, 'Aireys Inlet', Janjukian,  $\times$  2.

## PLATE 29

- Fig. 1-3—*Strongylocentrotus antiquus* sp. nov. (1) Adapical, (2) Lateral, (3) Adoral views of holotype AUGD 17014, 'Glenforslan', Longfordian.
- Fig. 4-5—Toxopneustid gen. et. sp. indet. (4) Test fragment P 18868, 'Aireys Inlet', Janjukian,  $\times$  2; (5) Test fragment P 18865, same locality,  $\times$  2.
- Fig. 6, 9—*Zenocentrotus peregrinus* sp. nov. (6) Broken interambulacral zone P 18473, 'Filter Quarry, Batesford', Longfordian or Batesfordian,  $\times$  2; (9) Broken interambulacral zone with attached poriferous tract P 18476, showing geniculation of interambulacral plates, same locality,  $\times$  2.
- Fig. 7—*Zenocentrotus peregrinus* sp. nov. (?) Radioles P 19652, 'Batesford', Longfordian or Batesfordian,  $\times$  2.
- Fig. 8—*Strongylocentrotus* sp. Test fragments P 18459, P 18468, 'Filter Quarry, Batesford', Longfordian or Batesfordian,  $\times$  2.